View metadata, citation and similar papers at core.ac.uk
brought to you by CORE
provided by Epsilon Archive for Student Projects

Examensarbete
Institutionen för ekologi

Despotic distribution in female fallow deer (*Dama dama*) groups

Madeleine Christensson

INDEPENDENT PROJECT, BIOLOGY

LEVEL D, 30 HP

SUPERVISOR: PETTER KJELLANDER, DEPT OF ECOLOGY, GRIMSÖ WILDLIFE RESEARCH STATION

COSUPERVISOR: ULRIKA ALM BERGVALL, DEPT OF ECOLOGY, STOCKHOLMS UNIVERSITY

EXAMINER: ANDERS JARNEMO, DEPT OF ECOLOGY, GRIMSÖ WILDLIFE RESEARCH STATION

Examensarbete 2010:4
Grimsö 2010

SLU, Institutionen för ekologi
Grimsö forskningsstation
730 91 Riddarhyttan

SLU, Sveriges lantbruksuniversitet/Swedish University of Agricultural Sciences
NL-fakulteten, Fakulteten för naturresurser och lantbruk/Faculty of Natural Resources and Agricultural Sciences
Institutionen för ekologi/Department of Ecology

Author: Madeleine Christensson
Title of the project: Despotic distribution in female fallow deer (*Dama dama*) groups
Title in Swedish: Finns det ett dominansförhållande mellan hindgrupper? – Och vad har det i så fall för betydelse?

Key words: Fallow deer, group living, rank, dominance, home range size, habitat preferrens

Supervisor: Petter Kjellander
Examiner: Anders Jarnemo

Title of the course: Independent project, biology
Code: EX0319
Extension of course: 30 hp
Level and depth of project: Advanced D
Place of publishing: Grimsö/Uppsala
Publication year: 2010

Program: Separate course

ABSTRACT
In a fallow deer population in south western Sweden was female group size and group composition estimated. A possible rank order between female groups and the effects of this was also investigated. By using GPS-position from 11 marked females was home range size, preferred habitats and distance to preferred habitats determined and tested for relationship to rank order. Mean female home range size was 2.92km^2 and preferred habitats were "Arable land", "Broad-leaved forest not on mire or open bedrock", and "Younger forest". Mean group size in mainly open areas was 72 individuals. Represented by the marked females there was a rank order found between female groups, and each marked female included in the rank study received a unique rank. There was a negative relationship between rank and home range size, the higher rank a female group did possess the smaller home range did it kept. Thus a high ranked group may not need to move over large areas to satisfy its requirements. This would mean less time to search for food and more time to forage and therefore an increased fitness. Further there was also a negative relationship between rank and area of preferred habitat, as high ranked female group kept a smaller area of the preferred habitats "Broad-leaved forest" and "Younger forest". This is related to a small home range that consists of smaller areas of preferred habitat in the same way a large home range consist of larger areas preferred habitat. This will however not mean that the low ranked group that keeps a large home range and large areas of preferred habitat always has access to all preferred habitats. Rather it is probably restricted at certain times by other groups with higher rank to one or several of these preferred areas and thus requires larger areas to alternate between. Finally, mean distance from home range centre to preferred habitat was smaller if the group had a higher rank. This is also related to the fact of a small home range in a high ranked group, where the distance to most habitats is shorter than in large home ranges as for a low ranked group.

Table of contest

Introduction

A home range is defined by the fact of that it is used, not how it is used (Barash 1982). Within this area there will be habitats that are used more frequently than others in relation to its availability, a so called habitat preference (Aarts et al. 2008). A home range, in contrast to a territory, is not defended against other individuals within the species. Consequently, home ranges do not have any strict boundaries and overlaps between individuals are common. But still there can be a core of the home range which is less likely to be shared with others (Barash 1982). A species that holds a home range part of the year can seasonally keep and defend a territory (Putman 1988). In mammals, non despotic spatial organisation (no dominance system) is quite common compared to e.g. birds that are more mobile than mammals, and have better potential to patrol a territory (Brown 1975). However, species which have a more selective food choice normally keep smaller territories. To be able to make the resources last in this small territory it have to live solitary and also be able to defend the resource (keeping the territory) (Putman 1988). If the food density is high enough, in relation to physiological requirements, it will be profitable to defend an area (Clutton-Brock & Harvey 1978). While in more indiscriminate bulk feeders, the home range grows according to increasing amount of food that is required, and there will be more individuals needed to search for the food and therefore will the group size increase (Putman 1988). This area will then be too large to defend as a territory, even for a group (Putman 1988). A home ranges also tends to be larger the poorer or patchier distributed the preferred habitat is (Turner et al. 1993).The size of a home range is therefore a result of many different factors; e.g. degree of cover, disturbance, population density and the season, which also affects the access of food (Chapman & Chapman 1975) and consequently the size of the group (Putman 1988). The utilisation of the home range can also change from day to day (Putman 1988) and even throughout the day, e.g. cervids generally use open areas more during the dark hours and closed areas during the bright hours (Borkowski & Pudelko 2007).

Animals that are gregarious are generally described to be so because it increases their fitness (see reference in Ebensperger & Hernán 2001). Whether to live solitary or to live in a group are a trade off-between advantages and disadvantages of these two ways of living. On one hand, the more individuals there are in a group the greater the chance is to detect predators. Less time per individual allocated to vigilance behaviours, less time spent to search for food and more time could be spent to forage (Lack 1954, Krebs & Davies 1987). If attacked, a large group can easily confuse the predator and make it harder to pick a specific victim, and it will also decrease the risk for the specific individual to be killed (Putman 1988). Depending on the habitat it can benefit to be more individuals in the search of food (Putman 1988). However, a disadvantage with a large group is of course the need for more food to support the group. An increased level of noise and a blocked view will affect the vigilance negatively and this disadvantage increase with the size of the group (Putman 1988). A larger group also increases their conspicuousness, as it is easier for a predator to find the group. But on the other hand for a predator it is harder to approach a large group undetected (Krebs & Davies 1987). These advantages and disadvantages are some of the mechanisms commonly suggested to affect the evolution of group living or solitary living, as it directly affects the fitness in different ways in each given case (Barash 1982, Putman 1988). When the chance of surviving and to improve in physical condition increase, this directly translates into increased fitness by a higher chance to breed. These trade off's will also be the basis for optimizing the group size

(Putman 1988). According to Sibly (1983) is an optimal size of a group (the group size is optimal when the fitness for the animal is optimal) never completely stable. Habitat openness and the amount of preferred habitat are described to have a positive effect on group size in large mammalian herbivores (Apollonio et al. 1998, Gerard & Loisel 1995, Hirth 1977, Putman 1988). In closed and poor habitats group size is expected to be smaller and in open and rich habitats it is expected o be larger. Population density will also affect the group size; particularly if a group size is unstable and change in random. If individuals meet in random and form groups, will this lead to an increasing of meetings and the group size will increase (Caughley 1964).

The distribution of animals is depending on the habitat's carrying capacity. If animals are free to move between habitats will the density of animals in each habitat balance their optimal fitness in relation to food availability, and this is referred to as the Ideal free distribution (Fretwell & Lucas 1970). A primary area which is the most optimal will attract most individuals until animal density will reach the limitation of its optimality. Thereafter will the individuals prefer other secondary areas which are now more optimal as long as every individual are free to choose the most optimal option (Sinclair et al. 2006). However, if individuals are not free to choose but narrowed or restricted by other individuals trough a dominance system, the rank order in this system will affect the individuals fitness positively or negatively (Sinclair et al. 2006). This is referred to as Ideal despotic distribution (Fretwell & Lucas 1970). High ranked individuals will then always have access to preferred habitats while lower ranked individuals will not.

A dominance system can be maintained between individuals in a solitary species, between individuals in a group (Putman 1988) and between different groups in a group living species (Kitchen et al. 2003). Dominance is an ability of an individual or group to control access of another individual or group to a resource (Brown 1975). A dominance system can deal with competition for mates and breeding opportunities, which is the most common competition between males and it can deal with competition for food and space which is the most common competition between females (Thouless & Guiness 1986). For a group living individual accepting to be subordinate to a higher ranked individual, there must be some advantages (increase of fitness) for the lower ranked, compared to not be included in the dominance system or the group (Barash 1982). Otherwise it will leave and then there will be no group or dominance system. In gregarious animals the older individuals usually seem to dominate the younger (Ozoga 1972, Clutton-Brock et al. 1986), but at a certain age their dominance declines (Ozoga 1972). As a female become older she is more likely to win over the older females, and to loose to the younger (Thouless & Guiness 1986). Female red deer (*Cervus elaphus)* lives in matrilineal groups where a dominance system is applied. Within these groups the aggressiveness toward relatives is less than between non-related females and fawns (Clutton-Brock et al. 1982). This reduced aggressiveness has been found between relatives in second and third degree generation and sometimes even further back (Ceacero et al. 2007). However the rank between the females is not decided by their kinship, but by age and body weight (Ceacero et al. 2007). And even if two non-related females meet, the older is the more dominant (Clutton-Brock et al. 1986). Thouless & Guiness (1986) found that when two red deer females from different home ranges met, the younger female won more often than it was expected to do. One explanation Thouless & Guiness (1986) gave for this was that older females are more likely to wander around than younger females are. The younger is more given to stay in their home range. Rank therefore seems to be site specific so that when animals wander around in areas they do not normally utilize, they feel insecure and do not have as high rank as within their ordinary home range. When meeting an unknown female inside a foreign home range, the unknown female (and home range owner) is more secure in that area and therefore she will have a higher rank, even though she might be younger than the intruder. Some tendencies of a dominance ranking between different female fallow deer groups have been observed (Putman 1988). However the picture is not clear as one group have been observed foraging together at the same time and place with other groups, but with some groups they don't (Putman 1988). This behaviour; ranking between different groups, however has not yet been scientifically investigated in female fallow deer.

The aim of this study is to investigate various aspects of group living and possible effects of a dominance system between female fallow deer groups. More specifically and based on GPS-marked adult females, the following aspects have been investigated: (1) the variation in group size and group composition, (2) home range size, (3) habitat preference, and (4) the level of temporal and spatial separation in home range overlap as a basis to assign a relative dominance rank between female group. If temporal or spatial separation between female home ranges or overlap area is found, is it hypothesized that the highest ranked group will (A) have the smallest home range and (B) the shortest mean distance to preferred habitat/s. In line with the Ideal despotic distribution theory (Fretwell & Lucas, 1970) will an animal which possess a high rank have access to highly preferred habitats (Spencer & Cameron 1983). Individuals with lower rank is more or less rejected from a food source, and consequently forced to move over larger areas to find other less preferred food sources (Clutton-Brock et al. 1982). Consequently, a high ranked female will have the smallest home range and save time and energy to move over large areas, this will then also mean smaller area of preferred habitat in the home range and the shortest mean distance to preferred habitat.

Study area

The study was carried out in Västra Götaland in south western Sweden, at the Koberg estate, latitude 58°N and longitude 12°E (Fig. 1). The Koberg estate constitutes 81.5km^2, an area divided in two parts by a fenced road. According to a vegetation survey (Winsa 2008) covering 54.35km^2 and SMD (a satellite generated digitized map, Svensk Marktäckedata) the area consist of 79% forest, 16% arable land and pastures, 2% of mires and marshes and 3% of lakes, ponds properties and parks (see Appendix 1 for a more detailed habitat composition). The density of fallow deer in the study area was in April 2006 32.7 animals/km^2. The population density of other ungulates in the area such as roe deer (*Capreolus capreolus*) was 1.7 animals/km^2 (Rydholm 2007) and moose (*Alces alces*) 0.65 animals/km^2 (Kjellander unpublished). The density of wild boar (*Sus scrofa*) is not estimated but considered as fairly high with an annual bag of 100-150 boars (Kjellander unpublished).

This study was mainly concentrated to the southern part of the estate in the Livered area that consists of a big part of coherent arable land. This is the part where the fallow deer population has its perhaps highest density in Sweden with 50 fallow deer/km^2 (Rydholm 2007).

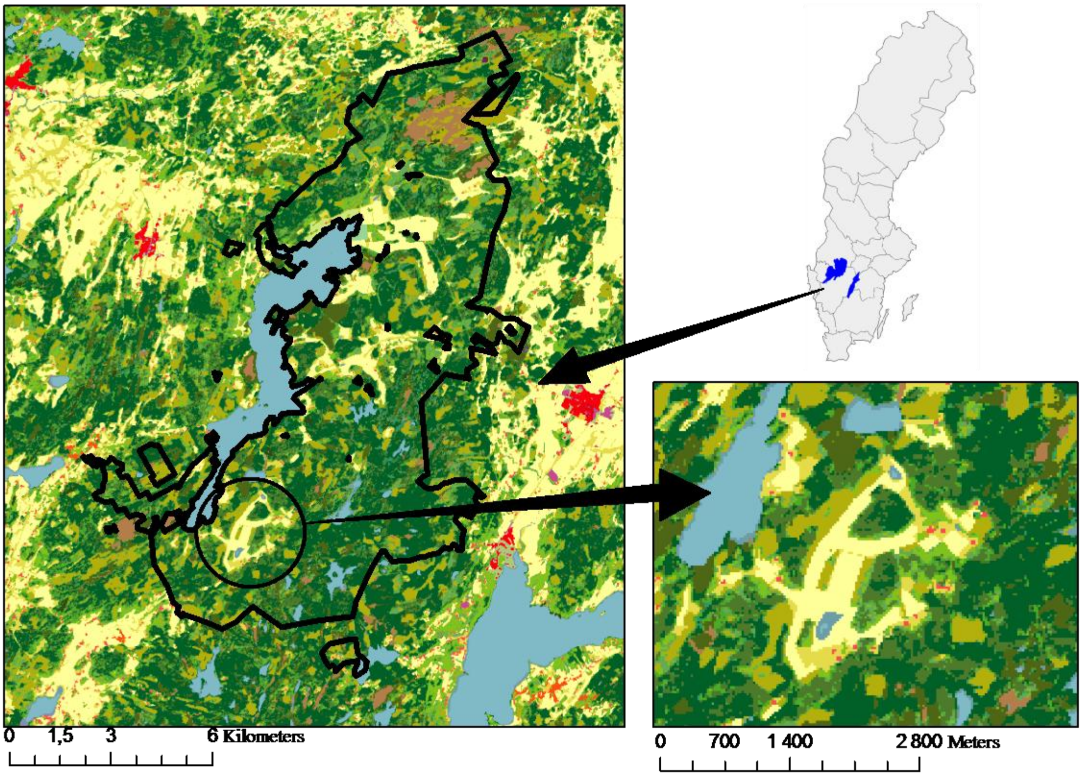

Figure 1. Right top corner: Sweden, showing the location of the Koberg estate. Left: The Koberg estate, showing the study area. The circle indicate the location of the high population density area Livered (see text). Right bottom: Close-up on Livered. Dark colours indicate forest habitat and bright colours indicate arable land and open areas.

Other ongoing research in the study area

The Roe deer - Fallow deer project

This study is part of a large study initiated in 2006 focusing on competition between fallow deer and roe deer. The project is lead by Petter Kjellander, Grimsö Wildlife Research Station, Riddarhyttan, Sweden. In the end this could generate more knowledge about how to manage the four nemoboreal Swedish deer species fallow deer, roe deer, moose and red deer (*Cervus elaphus*) when they live together in the same areas (Kjellander & Johansson 2006). Further, the main project also aims to investigate, for the first time in Sweden, various aspects of wild fallow deer ecology. In more recent time this part of the project has been extended to also incorporate aspects of behavioural ecology and animal personality in collaboration with Ulrika Alm-Bergvall at Edinburgh University.

Material

Study species – fallow deer (*Dama dama*)

The body weight of a female fallow deer is 35 – 60 kg, and for males 70-100 kg. Shoulder height of females are 70 – 80 cm and males ≥90 cm (Putman 1988). A newborn fawn has an average weight of 4.5 kg (Chapman & Chapman 1975).

The species is gregarious where the genders live in segregated groups outside the rut season (Villerette et al. 2006). The composition of the groups varies over the year (Chapman & Chapman 1975). Males live in bachelor groups most part of the year, but during the rut adult older males keep a small territory and form groups with the females (Chapman & Chapman 1975). Females with their progeny, sisters and other related females form groups and within this group one female is the leader (Chapman & Chapman 1975). Except these kinds of groups there can be mixed groups as mainly young but adult male occasionally join a female group (Putman 1988).

The size of a group depends on population size, habitat and season (Putman 1988). In a costal submediterranean environment in Italy, Apollonio et al. (1998) studied the group size of fallow deer. With four different kinds of group composition an average size in summer was for 1) a female and young-male group 3 individuals, 2) a female fawn group 4 individuals, 3) mixed group (adult males, females and fawns) 11 individuals and 4) adult male group 6 individuals. Large groups which are formed when foraging on larger open fields are not actually big social coherent groups but only occasionally groups, consisting of a few (or many) different core groups. These large group can consist of 70-100 individuals or more (Putman 1988).

The fallow deer is a polygamous species. The rut occurs in October – November and the female gives birth to one fawn (seldom two) in the middle of June to mid July. The female leaves the core group to a calm and safer place about one week before she gives birth (Carlström & Nyman 2005). At least in captivity the females also share some maternal care of the offspring in a core group based on close kinship (Ekvall 1998).

Fallow deer can be found in many different kinds of habitat, but tend to prefer deciduous and mixed forest, close to open areas such as agriculture land (Chapman & Chapman 1975). Factors as food availability, climate and season affect the size of the home range (Chapman & Chapman 1975).

The fallow deer is classified as an intermediate of grazers and browsers (Hofmann 1989). Grass is a big part of their diet, but the diet also contains leaves, bark, fruits, herbs, shoots from broad-leaved trees, sedge etc. Water is received mainly from the food, and the fallow deer seldom drink (Chapman & Chapman 1975). Feeding on open areas occur during all hours of the day but mainly during the darker hours, and their activity peaks take place at dusk and dawn (Chapman & Chapman 1975). The fallow deer have a great capacity to adapt to the climate and is found in many different habitats in line with their wide food choices (Chapman & Chapman 1975).

Males generally have larger home ranges than females (Chapman & Chapman 1975). In the United Kingdom the size of male home range varies between 0.5 – 2.5 km^2 and females between 0.5 – 0.9 km^2 (Putman 1988). In Southern Poland according to Borkowski & Pudelko´s (2007) study average male home range was 9.75 km^2 and female home range 2.1 km^2 and in New Zeeland average male home range is 1.89 km^2 and female 0.66 km^2 (Nugent 1994).

Today the distribution in Sweden is in Skåne, the most southern part of Sweden to approximately latitude 60°N, Uppland. In Småland and southern part of Västra Götaland the distribution is patchier. The most northern population described is situated at latitude 64°N, in the coast area of Västerbotten (Carlström & Nyman 2005). The highest concentrations of fallow deer are in Skåne, Östergötland, Södermanland and in an area in Västra Götaland just south of the big lake Vänern, (Carlström & Nyman 2005).

Method

During the period 25th of May to the 25th of August 2008 GPS-positions from 11 marked females (all ≥ 2 years old) were collected. The GPS-transmitters (Vectronic Aerospace GmbH, Berlin, Germany, model Pro-light, total weight of collar is 630g) were programmed to take one position every fourth hour (00.00, 04.00, 08.00, 12.00, 16.00 and 20.00). This schedule generated an average of 537 high quality (3D, ≥ 4 satellites) GPS-positions for each female during this study. At the most, 11 females have been used in this study. However, depending on the question not all females have been included in the different analyses.

Home range size and preferred habitat

Female home ranges were established using GPS-locations and the function MCP (Minimum Convex Polygon) in Arc View 3.3.

A habitat map was made based on the SMD map with a pixel size of 25x25 meters. To avoid having too many habitats represented by too small areas, some habitats were joined together as one in the calculation of preferred habitat. These clumped and rare habitats were “Broad-leaved forest on mires”, “Mixed forest on mire”, “Wet mire”, “Other mire”, “Lakes and ponds with open surface” and “Lakes and ponds with water surface being grown over”, these habitats are all related to water (from now called “Water related area”) and together they represent 5.0% of all available habitat (available habitat within the home ranges area). The same procedure was made with “Coniferous forest on open bedrock” and “Mixed forest on open bedrock” (from now called “Open bedrock related area”) representing 0.3% of all available habitat. (See table 1 in Appendix 1 for all habitats within the study area).

When preferred habitat was calculated a ratio between observed positions in a specific habitat and expected positions in the same habitat was obtained (Krebs 1999). First an index of preferred habitat was calculated and then the natural logarithm was taken;

$$ln\left(w_i = \frac{o_i}{p_i}\right)$$

Where:
w_i = index of preferred habitat
o_i = proportion of positions in specific habitat
p_i = expected number of position in a specific habitat

To obtain o_i the number of positions in the specific habitat (observed positions) was divided by the total number of position in the whole home range. p_i was obtained by dividing the proportion of the habitat in home range by the total number of position in the home range. This was made for each specific habitat for each specific female in the study. The indexes were imported to Stat View 4.5, where a One Sample Analysis t-test with a confidence interval of 95% and a hypothesized mean of 0, was made and split by habitat to gain preferred habitat/s.

Ranking

Seven of the eleven GPS-marked females were used in this part of the study. These seven are the “Livered-females” which were chosen because they lived in the same areas and have partly overlapping home ranges (Fig. 4). The four remaining marked female’s home ranges are situated much more to the north in the study area and are not in any contact with the Livered females.

There are many different methods to calculate the dominance ranking between animals in a group (see Tomback et al. 1989). The result from a given method can give different outcome depending on what kind of behaviour that is chosen to determine the ranking (Tomback et al. 1989). The competition for food within groups of grazing herbivores does often mean as little interferens as possible (see ref. within Thouless 1990). Thouless found that within a red deer group a subordinate female was more likely to leave a feeding site when a dominant female was approaching, than to stay (Thouless 1990). It has therefore in this study been used a method to calculate the rank order between the groups, that considers the GPS-positions in an overlap area between two females at a time. Since a female group follow the leader female (Focardi & Pecchioli 2005) it is in this study assumed that one female represents the group movements and home range. In this case it is the GPS-marked female that will represent the groups rank and behaviour. The ranking among the female groups has been made by comparing two females (i.e. groups) at a time. The overlap between the two females home range was accomplished with the MCP- and join function in Arc View 3.3. Secondly, locations from each female in the overlap area at each time, when there were no locations from the other female are in this study defined as “unique positions”. Such “unique positions” are the ones which have been used to calculate the rank. Three ways of calculating the rank were made: Rank 1, 2 and 3. The three different ranking calculations were compared by a Spearman Rank Correlation analysis to evaluate the robustness and generality of the methods.

Rank 1

This rank is based on how many positions that are expected (E) in the overlap area by each female. This was accomplished by calculating how big part of each females home range that constituted of the overlap area (a_x). These two overlap proportion areas from both females were added together ($a_1 + a_2$) to get a total overlap (b). The single overlap proportion was divided by b and then multiplied with the total number of observed “unique positions” from both female in the overlap (c). The number of expected positions in the overlap for each females was then $E = (a_x/b)*c$ (see example Fig. 2). These values were tested in Stat View 4.5 with a Contingency table – summary data to test if the observed number of unique positions significantly differed from the expected number (E) based on a_x (Fisher’s exact P-value). The outcome was evaluated in relation to if one female had significantly more position than the other female. The female with the significantly more “unique positions” in the overlap area became the winner and scored 1 point and the loser scored 0 points. In those cases when female pairs did not differ significantly, both female scored 0.5 points. This was made for all ID-combination (21 combinations). All the outcomes from the combinations were inserted into a cross table and all the victories and losses were counted for each female (Rayor & Chiszar 1978). To finally get the rank order, the sum of victories for each female was subtracted with the sum of losses; these numbers gave a ranking order between the females. The female which scored the highest number got the highest rank.

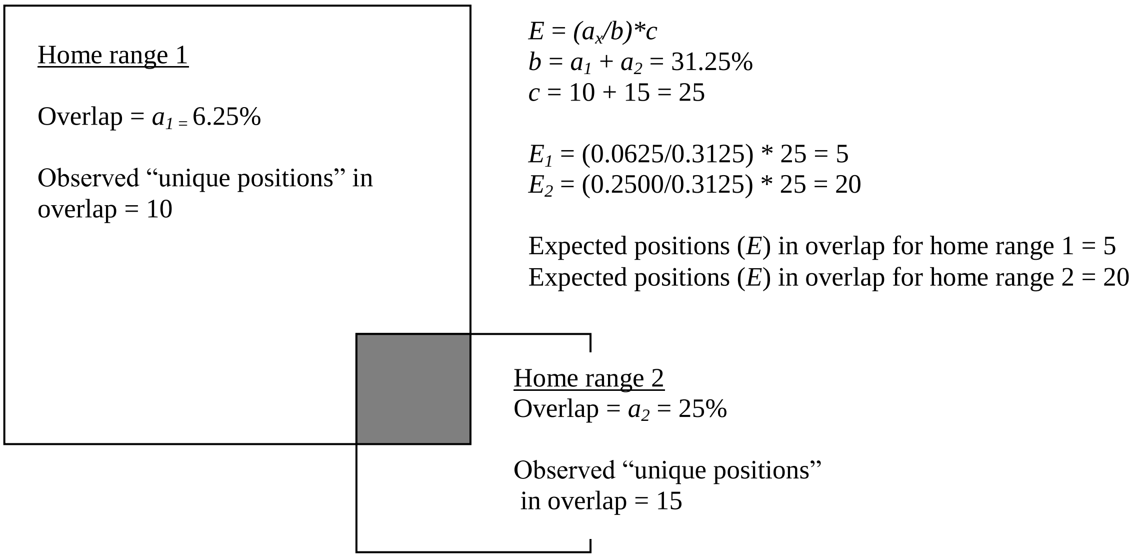

Figure 2. An example of the calculation of Rank 1. The squares represents the outer limit of two home ranges where expected and unique observed positions in the overlap for each female was tested for deviations between observed and expected distribution.

Rank 2

For each female the observed “unique positions” in the overlap was divided by expected position in the overlap (*E*). A percentage was given and used in the same kind of rank table (Rayor & Chiszar 1978) as for Rank 1. Instead of giving each female a score (0, 0.5 and 1), the Absolute value (Tomback et al. 1989), the given percentage, were put in the table. After this was the rank calculated as for Rank 1. The difference between the sum of all victories and the sum of all losses gave a number for each female which finally gave the rank order. A higher number gave a higher rank.

Rank 3

A triad comparison (Tomback et al. 1989) was made to estimate this rank. The calculations are based on the ranking received from Rank 2. If the difference between victories and losses, for each female, between the highest ranked and the second highest ranked individual was larger than the difference between the second and the third highest ranked, the first individual got the highest rank and a unique rank and the second individual got the second highest rank. If the difference wasn’t larger the second individual got the same rank as the first one (the highest ranked individual). Accordingly was a new triad made by moving down one step in the Rank 2 order. The second highest rank was now considered as the highest and the third got the second and so on until all individuals were ranked.

Distance to preferred habitats

The mean distance from the geometric centre (calculated in Arc View 3.3) of each female’s home range to the preferred habitat were calculated with the function Hawth’s Tools in Arc GIS 9.1. From the centre a distance to every polygon of each preferred habitat was calculated and divided by the number of polygons. Again was it the “Livered females” that was included in this analysis as the outcome later will be related to the ranking

Group size and group composition

The field work was carried out between the 8th of May and the 17th of June 2008. The group compositions for eight females were studied. A group was defined as a group if it according to the observer was clearly moving and separated from other individuals/groups. These eight individuals were chosen because the remaining three were very hard to observe and only visible a few times or not at all. The groups have mainly been observed in open areas, because of the limited visibility of a whole group in the forest.

Data that was collected when a defined group was found were; date and time when the observation started, coordinates where the observer was located, distance and bearing to the marked female, the ID of the marked female in the group, the total group size and the number of adult females, males and fawns it constituted. The study was divided in time intervals, were the first interval lasted from the time of the observers (or female's) arrival until the group composition changed in some way, e.g. groups merging, splitting up, single individuals leaving/arriving. Which of these events that took place was noted, and the next time interval started. The time for each interval was noted with an accuracy of one minute.

An average group size and group composition of a female group was calculated in Stat View 4.5 (descriptive statistics). Average size and composition of each female group was also calculated based on all observations of each specific group corrected for observation time.

Analysis

Individual female ranking was tested against home range size, access to preferred habitat, average distance to preferred habitat and group size. For all comparisons was the non-parametric Spearman Rank Correlation test used. Group size was also compared with the size of the home range and the area of preferred habitat in home range with a Spearman Rank Correlation.

Results

Preferred habitat

Three habitats within the home ranges were significantly preferred. Those were "Arable land" (*P* = <0.0001; *df* = 10), "Broad-leaved forest not on mire or open bedrock" (*P* = 0.0123; *df* = 10) and "Younger forest" (*P* = 0.0116; *df* = 10) (Fig. 3).

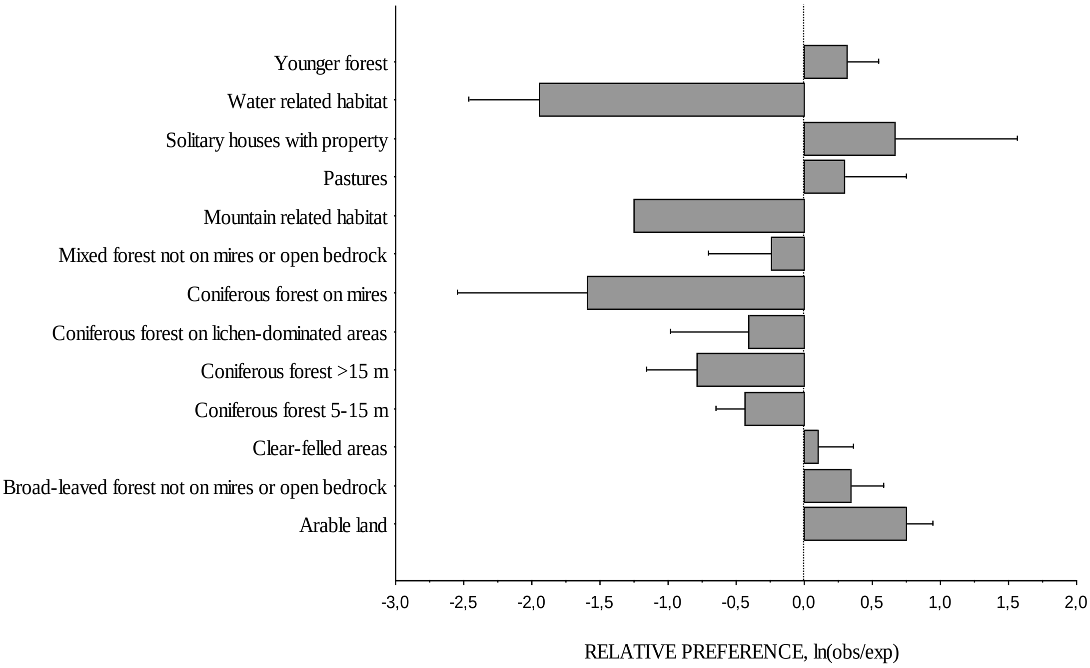

Figure 3. Habitat selection in 11 female fallow deer during the 25th of May and the 25th of August 2008 in south western Sweden. Three habitats were significantly preferred *; "Arable land", "Broad-leaved forest not on mire or open bedrock", and "Younger forest". One sample analyse t-test with a confidence interval of 95%.

Home range size

The average size of a home range area for female fallow deer during the study time was 2.92km^2± 0.65 (S.E), with a min-max range between 0.63km^2 and 6.47km^2 (Table 1). Figure 4 shows seven of the 11 marked females home range.

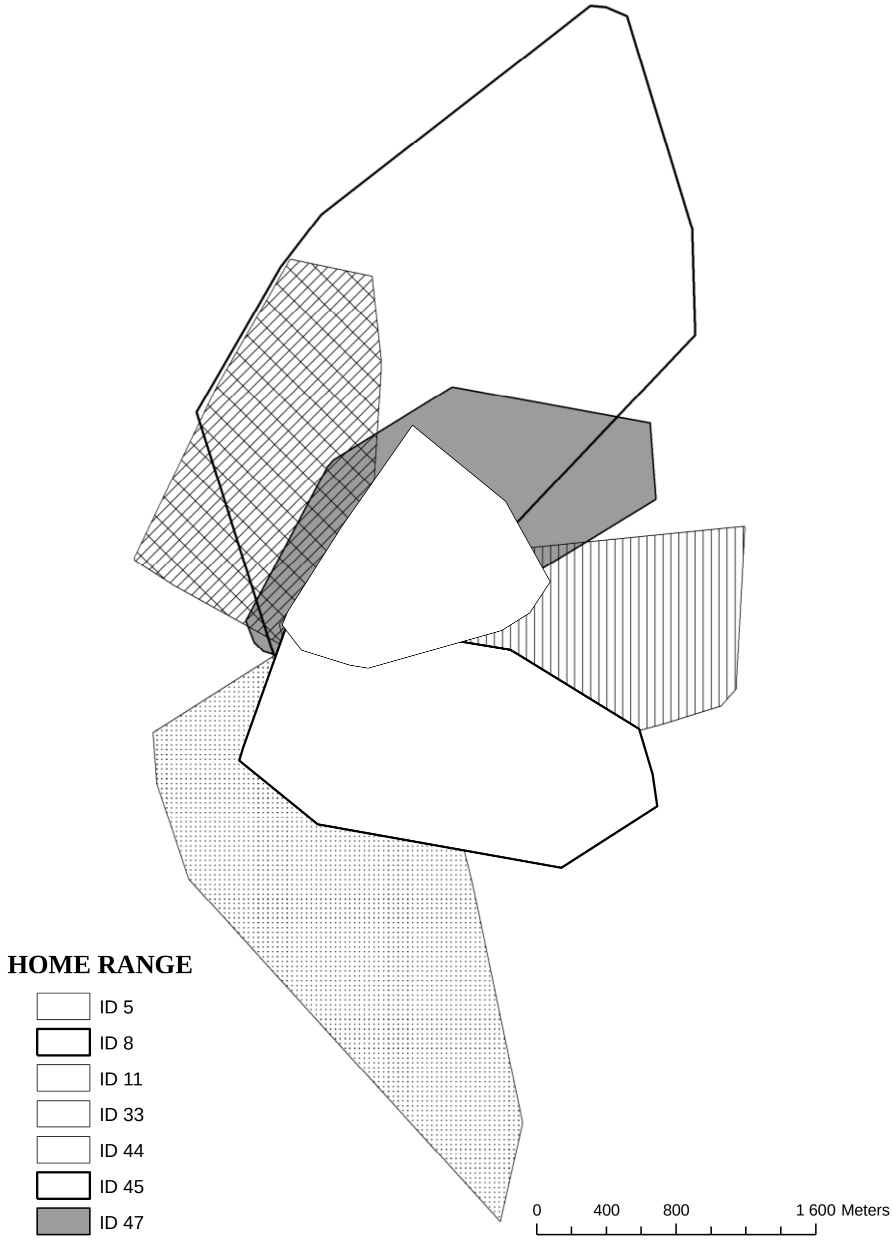

Figure 4. Seven home ranges from the GPS-marked “Livered female” fallow deer in south western Sweden in the southern part of the study area. In the centre of the map where all home ranges tend to overlap, is the central Livered area with large fields of arable land. All females do more or less overlap with each other.

Table 1. Home range size of 11 individual female fallow deer in south western Sweden and the percent of preferred habitats with in each home range.

ID	Home range area (km^2)	All preferred habitat in home range (%)
5	1.23	30.86
6	4.74	19.49
8	2.37	35.76
9	1.71	34.10
11	3.72	29.36
33	2.00	14.41
37	0.63	38.13
44	2.56	23.39
45	6.47	15.37
46	4.47	27.81
47	2.28	22.18
All ID	2.92	26.44

Overlap

Several of the female's home range at Livered did overlap with each other at some extent. Between 0.2% and 89.7% of the seven individual home ranges did overlap with another marked female (Table 1 in Appendix 2).

Ranking

A ranking order was found between the seven Livered female groups irrespective of ranking method. However with the method "Rank 2", each individual female was given a unique ranking score (Table 2 and 3.). This was not the case for "Rank 1" and "3", where two or more females ended up with the same score. Therefore only Rank 2 was used further on in this study. The different rankings were tested for significance and there was a significant relationship found in two out of three cases (Table 6). Calculations for rank 1, 2 and 3 are found in Appendix 2.

Table 2. Ranking table for Rank 2. Position in overlaps between two different female fallow deer at a time has been calculated and the percent of position of each female in each encounter is shown in the table. In a Vertical line (winners) sum of victories has been calculated for each female and in a horizontal line (losers) the sum of losses for each female have been calculated.

		W	I	N	N	E	R	S	
	ID	5	8	11	33	44	45	47	∑ Losses
L	5		31.7	55.6	161.1	11.6	9.2	54.9	324.1
O	8	135.0		165.7	123.0	131.6	8.8	122.6	686.7
S	11	26.9	58.2		200	61.0	13.9	109.1	469.1
E	33	62.1	72.8	0		59.4	10.8	179.8	384.9
R	44	142.7	70.7	156.6	131.8		30.3	150.4	682.5
S	45	117.3	133.4	149.5	127.6	127.6		135.2	790.6
	47	124.5	76.5	85.2	29.8	43.4	0		359.4
∑ Victories		608.5	443.3	612.6	773.3	434.6	73.0	752.0	

Table 3. Ranking order according to Rank 2 for marked females in the Livered area. The index which gives the ranking order is a result of the number of position in the overlap.
* High number equals high rank.

ID	5	8	11	33	44	45	47
Victories - Loses	284.4	-243.4	143.5	388.4	-247.9	-717.6	392.6
Rank order*	5	3	4	6	2	1	7

Distance to preferred habitat

Table 4. Mean distance (m), standard error and min. and max. distance to all preferred habitat for each individual female (ID) fallow deer and a mean distance for all females. For mean distance to each preferred habitat see Appendix 4.

ID	Mean distance (m)	Std. Err.	Min.	Max.
5	468	20.192	18	803
8	523	21.349	57	1175
11	969	23.510	334	1631
33	685	26.696	66	1088
44	592	27.069	5	1423
45	1006	29.728	32	2219
47	570	20.419	186	1179
All	758	12.691	5	2219

Group size and group composition

The mean group size for a female fallow deer group during the study time was 72 individuals per group with a span between 1 and 303 individuals (±*SE* = 1.098).
The mean group composition is given in table 5 and the group composition for each female's group is found in Appendix 3.

Table 5. Mean group size for all observed female (ID) groups and the mean number of individual of each category that compose a female fallow deer group in south western Sweden.

	Mean nr. of ind.	Standard error	Min.	Max.
Group size*	72	1.098	1	303
Females	39	0.658	1	177
Male	6	0.176	0	52
Fawn	12	0.206	0	53
Unknown	16	0.573	0	265

* Because of the different sampling units in the calculation of group composition and group size, the mean group size does not equal the exact sum of females, males, fawns and unknown.

Analysis

Rank – Home range size

The size of the home range did almost become significantly smaller with increasing female group rank (*P* =0.0662; *Rho* = -0.750) (Fig. 5 and Table 6*).*

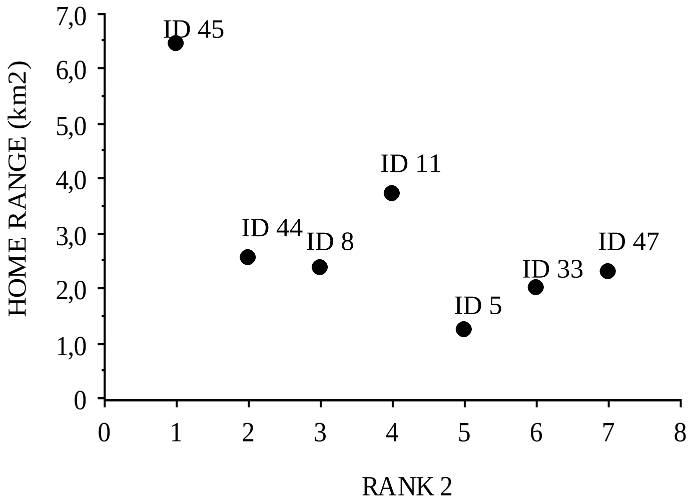

Figure 5. Home range size (km^2) vs. rank (Rank 2) in female fallow deer.

Rank – Area of preferred habitat in home range

Two of the preferred habitats did almost have significantly smaller size if the female group have a higher rank. These are "Broad-leaved forest not on mire or open bedrock" *P* = 0.0662; *Rho* = -0.750 and "Younger forest" *P* = 0.0802; *Rho* = -0.714; Fig. 6, Fig. 7 and Table 6). The total area of preferred habitat did not demonstrated any significant relationship with female group rank (*P = 0.1153*; *Rho* = -0.643; Table 6), neither did area of "Arable land" (*P = 0.2554; Rho = -0.464).*

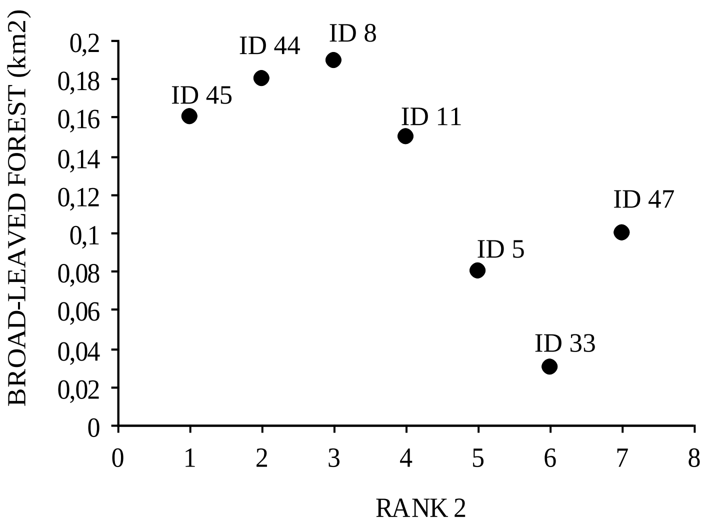

Figure 6. Area (km^2) of "Broad-leaved forest" in home range vs. rank (Rank 2) in female fallow deer.

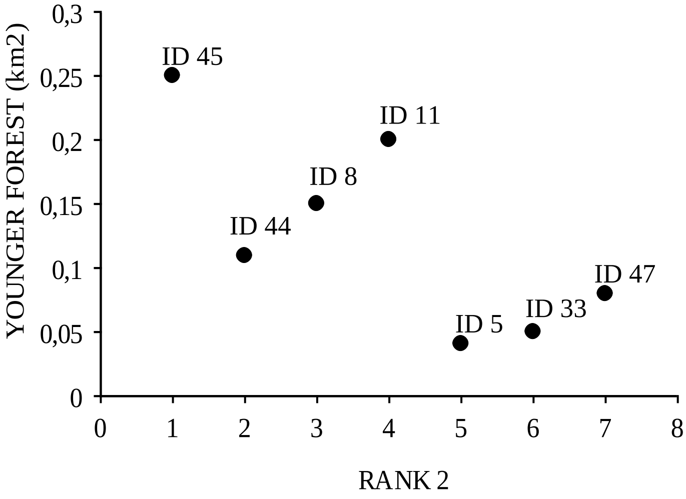

Figure 7. Area (km^2) of "Younger forest" in home range vs. rank (Rank 2) in female fallow deer.

Rank –mean distance to preferred habitat

A significant negative relationship between female rank and mean distance to all preferred habitat from the centre of the home range was found (*P* = <0.0001; *Rho* = -0.192) (Fig. 8 and Table 6). The distance to each habitat patch separately demonstrated a negative relationship for "Broad-leaved forest" and "Younger forest" (*P = <0.0001;Rho = -0.207, P = <0.0001; Rho = -0.172*). "Arable land" did not show any significance in this respect (*P = 0.1454; Rho = -0.250*).

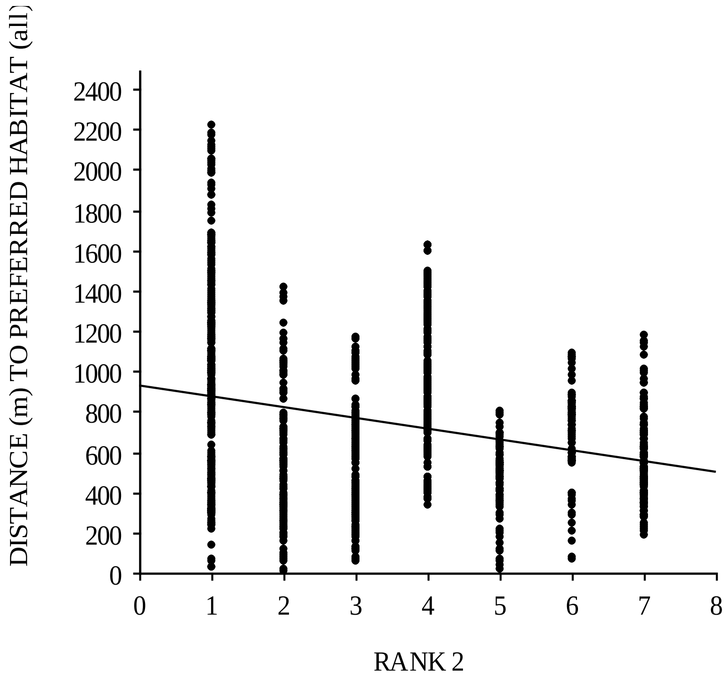

Figure 8. Distance (m) from the geometric centre in the home range to all preferred habitat patches in relation to the rank (Rank 2) of each individual female fallow deer (ID). Each point in the diagram represents one habitat patch.

Other comparisons
No significant relationship was found between group size and home range size, group size and the size (km^2) of all preferred habitat and group size and rank (Table 6).

Table 6. The table lists (P-values and Rho) if the rank order between different female fallow deer groups do correlate to the different measurements or not.

Comparisons /	\	P-value (Tied)	Rho (Corrected for ties)
Rank 2	Home range size	0.0662	-0.750
Rank 2	Area of preferred habitat (all)	0.1153	-0.643
Rank 2	Area of "Arable land"	0.2554	-0.464
Rank 2	Area of "Broad-leaved forest"	0.0662	-0.750
Rank 2	Area of "Younger forest"	0.0802	-0.714
Rank 2	Distance to all preferred habitat	<0.0001	-0.192
Rank 2	Distance to "Arable land"	0.1454	-0.250
Rank 2	Distance to "Broad-leaved forest"	<0.0001	-0.207
Rank 2	Distance to "Younger forest"	<0.0001	-0.172
Rank 2	Group size	0.3379	-0.429
Rank 2	Rank 1	0.0880	-0.696
Rank 2	Rank 3	0.0272	-0.902
Rank 1	Rank 3	0.0243	-0.920
Group size	Home range Size	0.4062	-0.371
Group size	Area of preferred habitat (all)	0.1417	-0.657

Discussion

In relation to the aims and hypotheses of this study was (aim 1) the mean size of a female fallow deer group 72 individuals with a variation between 1 and 303 individuals, (2) home range size varied between 0.63 km^2 and 6.47 km^2 with a mean size of 2.92 km^2; (3) out of 13 available habitats only three were found to be preferred, these were "Arable land", "Younger forest" and "Broad-leaved forest not on mire or open bedrock" and (4) a rank order between the seven different female groups was found and high ranked females groups kept the smallest home ranges (hypothesise A). Finally high ranked females did also have the shortest distance to preferred habitats from the centre of their home range (hypothesis B). These results will now be further discussed.

Group size and group composition
72 individuals as a mean group size of female fallow deer is a very high number compared to other studies (e.g. Apollonio et al. 1998). Several factors affecting the formation of large groups have been described. To begin with, there is the fact that group size in large mammal herbivores tend to increase with the habitat openness (Apollonio et al. 1998, Gerard & Loisel 1995, Hirth 1977 and Putman 1988). The habitat where the groups have been observed in this study is mainly in large open areas, mostly in arable land. The core groups which are smaller than these large groups merge at the open fields and this merged large group is only occasionally merged while foraging in open areas. This is a strategy to decrease the risk of being exposed to danger. If there are more individuals in a group the risk of being the victim

is smaller. A large group also increases the chance to detect a predator and the time allocated to vigilance per individual can thus decrease and the time to forage increase.

However, one factor that probably is very determinant is the high population density at the Koberg estate, which is maintained by careful management of the fallow deer population by e.g. extra feedings in the winter time (i.e. approximately 350 tonnes per winter). The variation also depends on the areas where the females live in the whole Koberg estate. In the northern part of the high density area (in the major project at Koberg), the density of fallow deer is lower than in the south southern part (Livered). ID 46 and 6 who have their home ranges in this northern part also have the smallest mean group size (Appendix 3). The variation in group size (and the mean size) could also be related to the time of the day. In the evenings and at night (not included in this study) and early mornings which is the time when the fallow deer is the most active and utilize open areas would be the time when the most animals is visible. This time is also the time when most of the observations have been made. However, some observations have been made during midday. The midday observation times would then be when the groups are small, and perhaps more limited to the core groups. Even though these examples are considered there can be one other thing affecting the group size; the problems for the observer to separate the different groups on the field. If the distances between the groups have been, according to the observer, short enough for two smaller groups to be considered as one or not. Or in one group were parts of the group just happen to have a larger distance at the moment.

Another question is if these female groups are “stable in time”. As mentioned there was some difficulties calculating and defining the group size in field. Since group size variation is large it is obvious that a group is not stable and it does not constitute the same individuals all the time. However, the smaller core group tends to be more stable. These core groups are pieces of the large group but what this core group constitutes of cannot be established in this study. It is still unresolved if it is the same core groups that merge and form larger groups or if it is different groups from time to time. To answer that question would require a larger number of marked individuals. In any case and according to the ranking order found in this study it seems to be more or less the same groups merging.

Home range size

The size of the home ranges is large, ranging from 0.63 km^2 – 6.47 km^2 compared to other studies on fallow deer. In the United Kingdom (Putman 1988) and New Zeeland (Nugent 1994) the size in female fallow deer home range varies between 0.5 and 0.9 km^2. In Poland (Borkowski & Pudelko 2007) the average size is 2.1 km^2 which is more similar to this study (mean 2.92km^2), however that study reported an annual home range size and the study area mainly consisted of Scots pine (*Pinus silvestris*) 75% and a smaller amount of Oak (Q*uercus robur*), Birch (*Betula verrucosa*) and Alder (*Alnus glutinosa*). The habitat at Koberg is very mixed but the largest part constitutes of coniferous forest, 44%, and arable land, 12% (*Appendix 1*). Maybe the differences between the two study areas (Koberg and Poland) are not that big in composition of the habitat to explain a difference big as that in the home range size. The patchiness of the habitat could also makes a difference.

However, the time period differs with 9 months. Possibly seasonal movements will make an annual home range larger and thus making the Koberg home range sizes even larger. According to Putman (1988) would home range size be larger in winter and autumn than in spring and summer because of the limited food resources, as the deer need to move over larger areas to gain the food they need. However, in the polish fallow deer (Borkowski & Pudelko 2007) the largest home range was found in spring and summer. The present study only investigates summer home range size and with no consideration to the other seasons and maybe there is a big difference between the seasonal home ranges in line with Borkowski & Pudelko (2007).

Further, the population density might be a factor affecting range size. More individuals and large groups increase the need of more food and thus should the movement of the animals increase (Putman 1988). However, when looking on the different female home ranges in this study, the largest is found in the northern part of the south study area with the lowest density (with the exception ID 45).

Whether the patchiness of the habitat effect this is not investigated in this study, but home range tend to be larger the patchier or poorer the preferred habitat is (Turner et al. 1993). ID 45 who's home range is the largest of all female, lives in the mid-south intermediate density area. Her visits in the southern high density Livered area is only occasional, as her normal and most used area is her mid and north part of her home range. Maybe does this makes the mean home range size in this study much larger than it should have been with at larger number of marked individuals.

Other methods to determine individual home ranges that only include the areas they actually use, might have generated a different result. Home range size would definitely decrease for all individuals and perhaps also the area of some preferred habitats. However, it is unclear if this would have strengthened the conclusions even further, or made them weaker.

Preferred habitats

The preferred habitats in this study ("Arable land", "Broad-leaved forest not on mire or open bedrock" and "Younger forest") tend to be similar to other studies i.e. deciduous and mixed forest, meadows, and agriculture land (Chapman & Chapman 1975, Borkowski & Pudelko 2007, Apollonio et al. 1998, Putman 1988). This reflects their food choice of grass and crops from the agriculture land, shoots from deciduous trees and bark from younger trees.

Ranking

In this study there were three ways of testing a possible rank order between the female groups, one of these was finally used. This rank was chosen because it gave a unique rank score for each female group, which made it easier to handle when different analyses were made. Rank 1 was considered to be usable since the score system was based on what amount of locations that was expected in the overlap and is based on how big part of the home range the overlap represented. If a large home range is compared with a small home range, the overlap area will be a smaller proportion of the large home range than in the small home range. This means that there will be fewer locations in the overlap from groups which holds larger home range, and the group with the small home range would have more locations in the overlap zone. However as mentioned before, this rank gave the same rank score to more than one female group. Therefore was alternative methods used i.e. Rank 2 and 3.

Rank 2, which was finally used in the analysis, is based on the same as in Rank 1 but a percent of how many positions that was found in the overlap compared to the expected was used. As Rank 2 gave the sum of victories minus the sum of losses, it resulted in very small difference between some female groups (Table 3). E.g. between rank order 7 and 6 (ID 47 and 33) there are only 4.2 units differing. Are these individuals maybe supposed to have the same rank? Between other groups the difference is much larger, e.g. between the rank order 1 and 2 (ID 45 and 44) it differs with 469.7 units. Maybe is therefore the interpretation that rank order 6 is as much dominant over rank order 5 as rank order 2 is over rank order 1 wrong (Table 5 in Appendix 2)?

In the group size observations there were six observations where marked females were found in the same group. In three of these occasions ID 47 and 33 were in the same group, and none of the observations was the highest and lowest ranked seen in the same group.

Finally a third rank calculation was made, Rank 3 (Table 5 in Appendix 2). This considers the differences between the different rank orders (as discussed above). If the indexes don't differ enough, two different female groups gained the same rank order, e.g. ID 47 and 33.

To make sure that these three different rank calculations (1, 2 and 3) didn't differ too much they were tested against each other and two out of three cases did correlate to each other (the third did almost correlate). Rank 2 was chosen to represent the ranking between the female groups. To make the results better in this study a larger sample size would have been desirable. Seven females in rank calculations are few and to have one female representing her whole group might not be a valid assumption. More GPS-marked females and more than one in the same permanent core group would be very interesting for the future to use.

Analysis

Rank order effects on home range size

Maybe the most interesting results in this study were the investigated relationships between rank order and home range size. In line with the hypotheses, a negative trend was found, that a high ranked group keeps a smaller home range compared to a lower ranked group. Maybe as a first thought it is easy to believe that a high rank equals to a large amount of something of high value. However, high ranked groups/individuals in this case choose and have a continuous and reliable access to the best areas of food and cover. They have all their needs i.e. food and cover close and do not need to move over large areas to satisfy their requirements of resources. In this way they save energy and time, which they instead can use to increase their fitness, e.g. more time to forage, rest and perhaps also vigilance? A low ranked group/individual do not have unlimited access to the best areas, and to full fill their needs of food and cover they need to move over larger areas, to pick small pieces of the good in different places. This will result in less time to forage, more energy loss and consequently a lower fitness.

ID 45, discussed earlier in this section, ended up with the lowest rank of all females and do, as mentioned before keep the largest home range of all. Her rare and occasional visits at the high density Livered area would likely have something to do with her low rank. As she normally doesn't seem to have access to Livered with the large areas of the most preferred habitat "Arable land", it is worth the chance to try to get a bite of it every now and then. But for some reason she doesn't stay for long. This argument is in line with Thouless & Guiness (1986) as they implied that individuals that move around in unknown or less known areas, are more insecure and lose the rank they posses in their ordinary home range. In this study her (ID 45) rank situation according to other females that have a home range closer to her core area, have not been possible to investigate. ID 45 was not included in the study of group size and composition because of the hardness to observe her in field. However, in another study she was observed in the Livered area and as an overall impression of her behavior she seemed particular nervous when feeding at Livered. The data of this observation shows that her time spent to vigilance increased from 2% when observed in her core area, to 17% when observed at Livered (Bergvall & Kjellander unpublished). The mean proportion of time spent to vigilance for all marked and observed females in that study (Bergvall & Kjellander unpublished) is 3%.

The information generating the rank and home range size etc. is gained from the same data (i.e. GPS-positions). The method to produce independence between these variables was to correct each individual rank calculation for home range size (see methods). However, beside this obvious dependence that was corrected for, there might be more subtitle effects that is affecting the results of the rank calculation. A method to obtain a rank that is totally independent of the GPS-positions would therefore be desirable. Such a method could possibly be to observe the groups and collect data of their behavior when interacting with other groups.

Rank order effects on area of preferred habitat and distance to preferred habitat

The area of preferred habitat in the home range demonstrated a close to significant and negative relationship with the rank order in two of the three estimates of preferred habitats; “Broad-leaved forest” and “Younger forest”. If the female group had a higher rank it also had less area of these preferred habitats. This is obviously related to the size of the home range, if the home range is small then there can only be certain area of preferred habitat (maximum 100%). But why does a low ranked group have more area of preferred habitat? It would be profitable to have a large area of preferred habitat. But considering the earlier discussion about a low ranked group/individual that have to move over large areas to satisfy its resource needs, this doesn’t mean that it have access to every patch of habitat in its home range. The home range has been calculated with the minimum convex polygon method which means that the 100% border line has been drawn between the outermost positions. This can mean that even though don’t having access to it according to their low rank, it is included in the subjective construction of the home range. So the actual access to the preferred, available and used habitat in reality is maybe much smaller than the habitat determined by minimum convex polygon home range. And perhaps even smaller than the high ranked individuals with unlimited access.

The second hypothesis was that a high ranked group will have a shorter distance to preferred habitat. The data supports this hypothesis as there was a significant and negative relationship in all habitats combined and in two (“Broad-leaved forest” and “Younger forest”) out of the three preferred habitats separately. However, again this result relates to the previous argumentation about size of the home range and area of preferred habitat. A smaller home range by default will have shorter distances to all habitats irrespective of it preference.

In a high ranked group it might not matter if the preferred habitat is located in or close to the core area or closer to the edge, since the whole home range might be considered as a core area and everything is within short distance. However in a home range of a low ranked group everything is at a larger distance as the home range is larger and preferred habitats accordingly at further distance. If most of the preferred habitat was close to the centre then the group wouldn’t need to keep the distant parts of the area and the home range would become smaller in size.

No significant relationship between distance to “Arable land” and rank was found. This could raise a question about utilization of this habitat by the low ranked groups. The rank was calculated through the overlap areas, where the most common habitat was “Arable land”. Do the low ranked groups have to use exactly this area? Maybe they have “Arable land” in other parts of their home range, closer to the centre of the home range? An explanation for this could be that the distribution of "Arable land" in the study area is very concentrated to a few places. This habitat is mostly found in large coherent fields. There are however, less fragments of this preferred habitat than there is of the other two preferred habitats. Comparing the number of fragments of "Arable land" in the home range between the highest and lowest ranked group , the high ranked had 3 fragments with at mean size of 0.11km^2, and the low ranked had 8 fragment with mean size of 0.07km^2. The largest fragment in the low ranked home range is in the overlap. Therefore it is believed that the low ranked group have to use the overlap area in addition to the smaller fragments, to satisfy their need of resources.

Other comparisons

Finally, one would expect that a large group needs a larger area to satisfy their needs of resources. Especially should the area of preferred habitat increase with a larger group as there will be more individuals to feed. In line with this was the group size investigated in relation to several different variables gained from this study, such as rank, home range size and area of preferred habitat However, none of these comparisons did significantly relate to group size. The most obvious explanation to this negative result is probably to find in the definition of a group in this study (see group composition in section method and discussion). Probably was the core group size overestimated, as it is impossible to determine if they were merged core groups on the open forages areas or not. If there would be some relationships between group size and home range size, a large home range size for the larger groups (many merged core groups) would probably be expected. This would also apply to the area of preferred habitat since the area of preferred habitat relates to the home range size (see Rank order effects on area of preferred habitat and distance to preferred habitat in discussion).

Acknowledgements

Fist of all I want to thank my supervisor Petter Kjellander at Grimsö research station, SLU, for a great support and help throughout this thesis, and most of all for giving me the opportunity to do this work on fallow deer. I also want to thank my assistant supervisor Ulrika Alm Bergvall at Stockholm University, for great help and ideas. I want to thank Gustaf Samelius for sharing his knowledge in GIS-programs, and Anders Jarnemo for proofreading my paper. A huge tanks to Eva Immler and Sabine Müller for all help with my field work at Koberg. Not least for a very good company and for giving me a great summer at Koberg, for all the fun times and happy faces. I also want to thank the owner and the staff at the Koberg estate for letting me carry out my field work at this beautiful place. And to all the fallow deer in the area, especially ID 5, 6, 8, 9, 11, 33, 37, 44, 45, 46 and 47. Thank you so much for being you and letting me and so many other wacky fieldworkers, students and researcher observe you day in and day out.

References

Aarts, G., MacKenzie, M., McConnell, B., Fedak, M,. Matthiopoulos, J. 2008. Estimating space-use and habitat preference from wildlife telemetry data. Ecography 31: 140-160

Apollonio, M., Focardi, S., Toso, S. & Nacci L. 1998. Habitat selection and group formation pattern of fallow deer *Dama dama* in a submediterranean environment. Ecography 21: 225-234

Barash, D. 1982. Sociobiology and behavior. 2nd ed.. Elsevier Science Publishing Co., Inc.

Borkowski, J. & Pudelko, M. 2007. Forest habitat use and home range size in radio-collared fallow deer. Annales zoologici Fennici. 44: 107-114.

Brown, J.L. 1975. The evolution of behaviour. W.W. Norton & Company Inc. New York.

Carlström, L. & Nyman, M. 2005. Dovhjort. Jägareförlaget/Svenska Jägareförbundet, Kristianstad Boktryckeri AB, Kristianstad

Caughley, G. 1964**.** Social organization and daily activity of the red kangaroo and the grey kangaroo. Journal of Mammalogy. 45: 429-436.

Ceacero, F., Landete-Castillejos, T., García, A. J., Estévez, J. A. & Gallego, L. 2007. Kinship Discrimination and Effects on Social Rank and Aggressiveness Levels in Iberian Red Deer Hinds. Sección de Recursos Cinegéticos, IDR, Universidad de Castilla-La Mancha, 02071, Albacete, Spain.

Chapman, D. & Chapman, N. 1975. Fallow deer. New ed. 1997. Coch-y-bonddu Books, Machynlleth.

Clutton-Brock, T. H., Albon, S. D. & Guinness, F. E. 1986. Great expectations: dominance, breeding success and offspring sex ratios in red deer. Animal Behaviour. 34: 460-471.

Clutton-Brock, T.H., Guinness, F.E. & Albon, S.D. 1982. Red deer behaviour and ecology of two sexes. Edinburgh University Press 22 George Square, Edinburgh.

Clutton-Brock, T.H. & Harvey, P.H. 1978. Mammals, recourses and reproductive strategies. Nature. 273: 191-195.

Ebensperger, L.A. & Hernán, C. 2001. On the evolution of group-living in the new world cursorial hystricognath rodents. Behaviour ecology. 12: 227-236.

Ekvall, K. 1998. Effects of social organization, age and aggressive behaviour on allosuckling in wild fallow deer. Animal behaviour, 56: 695-703.

Focardi, S. & Pecchioli, E. 2005. Social cohesion and foraging decrease with group size in fallow deer (Dama dama). Behavioral ecology and sociobiology. 59: 84–91

Fretwell, S.D. & Lucas, H.L. 1970. On territorial behaviour and other factors influencing habitat distribution in birds. Acta Biotheoretica. 19: 16-36.

Gerard, J-F. & Loisel, P. 1995. Spontaneous Emergence of a Relationship between Habitat Openness and Mean Group Size and its Possible Evolutionary Consequences in Large Herbivores. Journal of Theoretical Biology. 176: 511-522.

Hirth, D. H. 1977. Social behavior of white-tailed deer in relation to habitat. Wildlife Monographs. 53.

Hofmann, R.R. 1989. Evolutionary steps of ecophysiological adaptation and diversification of ruminants: a comparative view of their digestive system. Oecologica. 78: 443-457

Kitchen, D.M., Cheney, D.L. and Seyfarth, R.M. 2003. Factors mediating inter-group encounters in savannahbaboons (papio *cynocephalusursinus*). Behaviour 141: 197-218

Kjellander, P., Johansson, Ö. 2006. Hur påverkar dovvilt och rådjur varandra? Svensk Jakt. Nr. 11.

Krebs, J.R. & Davies, N.B. 1987. An Introduction to behavioural ecology. 2nd ed. Blackwell scientific publications. Osney Mead, Oxford.

Krebs, C.J. 1999. Ecological methodology – 2nd ed. Addison Wesley Longman.

Lack, D. 1954. The natural regulation of animal numbers. Oxford University Press, Amen House, London E.C.4.

Nugent, G. 1994. Home range size and its development for fallow deer in the Blue Mountains, New Zeeland. Acta Theriologica. 39: 159 -175.

Ozoga, J. J. 1972. Aggressive behavior of white-tailed deer at winter cuttings. Journal of Wildlife Management. 36: 861-868

Putman, R. J. 1988. The natural history of deer. Christopher Helm (publishers) Ltd, Imperial House, 21-25 North Street, Bromley, Kent BR1 1SD.

Rayor, L.S., Chiszar, D. 1978. Comparability of dominance indices in captive pigtail macaques (*Macaca nemestrina*). Bulletin of the Psyehonomic Society. 12: 468-470.

Rydholm, M. 2007. Hur ska dov och rådjur leva ihop? Svensk Jakt. 8: 74-77.

Sibly, R.M. 1983. Optimal group size is unstable. Animal Behaviour. 31: 947-948

Sinclair, R.E., Fryxell, M. & Caughley, G. 2006. Wildlife ecology, conservation and management. 2nd ed.. Blackwell Publishing 350 Main Street, Malden, MA 02148-5020, USA.

Spencer, S.R. & Cameron, G.N. 1983. Behavioral dominance and its relationship to habitat patch utilization by the hispid cotton rat (*Sigmodon hispidus*). Behavioral ecology and sociobiology. 13: 27-36

Thouless, C. R. & Guiness, F. E. 1986. Conflict between red deer hinds: the winner always wins. Large animal research group, Department on zoology, Cambridge CB3 0DT, U.K.

Thouless, C.R. 1990. Feeding competition between grazing red deer hinds. Animal behaviour. 40: 105-111.

Tomback, D.F., Wachtel, M.A., Driscoll, J.W. & Bekoff, M. 1989. Measuring Dominance and Constructing Hierarchies: An Example Using Mule Deer. Ethology 82: 275-286

Turner, M.G., Wu, Y., Romme, W.H. & Wallace, L.C. 1993. A landscape simulation model of winter foraging by ungulates. Ecological modelling. 69: 163-184.

Villerette, N., Helder, R., Angibault, J.M. & Cargnelutti, J.F.G. 2006. Sexual segregation in fallow deer: are mixed-sex groups especially unstable because of asynchrony between the sexes? Comptes Rendus Biologies. 329: 551-558.

Winsa, Marie. 2008. Habitat selection and niche overlap – A study of fallow deer (*Dama dama*) and roe deer (*Capreolus capreolus*) in south western Sweden. MSc thesis, Department of ecology, Swedish university of agricultural sciences. Report no 2008:11.

Appendix 1. Habitat

Table 1. Habitat composition in the major study area at Koberg in south western Sweden (Winsa, 2008).

Habitat nr.	Habitat	Habitat composition in study area (%)
5	Solitary houses with property	0.33
19	Non-urban parks	0.36
30	Arable land	12.46
32	Pastures	3.97
40	Broad-leaved forest not on mires or open bedrock	3.37
41 *[1]	Broad-leaved forest on mires	0.10
43	Coniferous forest on lichen-dominated areas	2.51
44	Coniferous forest 5-15 m	15.24
45	Coniferous forest >15 m	28.79
46	Coniferous forest on mires	5.86
47 *[3]	Coniferous forest on open bedrock	0.48
48	Mixed forest not on mires or open bedrock	5.69
49 *[1]	Mixed forest on mire	0.28
50 *[3]	Mixed forest on open bedrock	0.02
54	Clear-felled areas	9.97
55	Younger forest	6.87
70 *[2]	Water dominated areas	1.72
71*[1]	Wet mire	-
72*[1]	Other mire	-
81*[1]	Lakes and ponds open surface	1.15
82*[1]	Lakes and ponds surface being grown over	0.85

*[1] Water related habitats. These habitats are combined as one in the present study of preferred habitat.
*[2] The values in habitat 70 also include habitat 71 and 72 (Winsas 2008)
*[3] Open bedrock related habitat. These habitats are combined as one in the study of preferred habitat.

Table 2. Total habitat composition of all eleven female fallow deer home ranges in the present study.

Habitat nr.	Habitat	Area (km^2)	% of all home range areas
5	Solitary houses with property	0.10	0.32
30	Arable land	4.70	14.61
32	Pastures	1.63	5.05
40	Broad-leaved forest not on mires or open bedrock	1.29	4.03
43	Coniferous forest on lichen-dominated areas	0.33	1.02
44	Coniferous forest 5-15 m	5.10	15.85
45	Coniferous forest >15 m	8.44	26.26
46	Coniferous forest on mires	2.93	9.10
48	Mixed forest not on mires or open bedrock	1.51	4.71
54	Cleare-felled areas	2.70	8.41
55	Younger forest	1.72	5.34
-	Water related areas	1.62	5.03
-	Mountain related areas	0.09	0.27

Appendix 2. Data for rank calculations.

Table 1. Calculations for Rank 1 and 2

ID-comb.	% overlap in home range Sing. = a_x Tot. = b	Unique pos. in overlap Tot. = c	Expected nr. of positions E $((a_x/b*c))$	P-value (Fisher's exact) (exp. = obs.)	Scores in Rank 1-table	Unique pos. in overlap/exp. pos. in overlap (E) (Rank 2)
5	13.2	108	80		1	135.0
8	6.9	13	41		0	31.7
Total	20.1	121	121	<0.0001		
5	5.2	30	26		0.5	26.9
11	1.7	5	9		0.5	55.6
Total	6.9	35	35	0.3707		
5	14.2	18	29		0	62.1
33	8.8	29	18		1	161.1
Total	23	47	47	0.0386		
5	57.3	382	268		1	142.7
44	27.7	15	129		0	11.6
Total	85	397	397	<0.0001		
5	76.9	266	227		1	117.3
45	14.7	4	43		0	9.2
Total	91.6	270		<0.0001		
5	89.7	230	185		1	124.5
47	48.6	55	100		0	54.9
Total	138.3	285	285	<0.0001		

Appendix 2. Data for rank calculations.

Table 1 sequel. Calculations for Rank 1 and 2

ID-comb.	% overlap in home range Sing. = a_x Tot. = b	Unique pos. in overlap Tot. = c	Expected nr. of positions E $((a_x/b*c))$	P-value (Fisher's exact) (exp. = obs.)	Scores in Rank 1-table	Unique pos. in overlap/exp. pos. in overlap (E) (Rank 2)
8	44.3	81	139		0	58.2
11	28.2	147	89		1	165.7
Total	7.5	228	228	<0.0001		
8	1.9	1	1		0.5	72.8
33	2.2	2	2		0.5	123.0
Total	4.1	3	3	>0.9999		
8	35.2	112	158		0	70.7
44	32.6	193	147		1	131.6
Total	67.8	305	305	0.0002		
8	12.9	165	124		1	133.4
45	4.7	4	45		0	8.8
Total	17.6	169		<0.0001		
8	7.5	24	31		0.5	76.5
47	7.8	40	33		0.5	122.6
Total	15.3	64	64	0.2840		
11	0.2	0	1		0.5	0
33	0.4	2	1		0.5	200
Total	0.6	2	2	>0.9999		

Appendix 2. Data for rank calculations.

Table 1 sequel. Calculations for Rank 1 and 2.

ID-comb.	% overlap in home range Sing. = a_x Tot. = b	Unique pos. in overlap Tot. = c	Expected nr. of positions E $((a_x/b*c))$	P-value (Fisher's exact) (exp. = obs.)	Scores in Rank 1-table	Unique pos. in overlap/exp. pos. in overlap (E) (Rank 2)
11	6.9	30	19		1	156.6
44	10.0	17	28		0	61.0
Total	16.9	47	47	0.0384		
11	6.1	75	50		1	149.5
45	3.5	4	29		0	13.9
Total	9.6	79	79	<0.0001		
11	2.4	11	13		0.5	85.2
47	3.9	23	21		0.5	109.1
Total	6.3	34	34	0.8000		
33	5.3	17	13		0.5	131.8
44	4.2	6	10		0.5	59.4
Total	9.5	23	23	0.3534		
33	80.3	267	209		1	127.6
45	24.8	7	65		0	10.8
Total	105.1	274	274	<0.0001		
33	22.8	36	121		0	29.8
47	20.0	191	106		1	179.8
Total	42.8	227	227	<0.0001		

Appendix 2. Data for rank calculations.

Table 1 sequel. Calculations for Rank 1 and 2.

ID-comb.	% overlap in home range Sing. = a_x Tot. = *b*	Unique pos. in overlap Tot. = *c*	Expected nr. of positions *E* $((a_x/b*c))$	P-value (Fisher's exact) (exp. = obs.)	Scores in Rank 1-table	Unique pos. in overlap/exp. pos. in overlap (*E*) (Rank 2)
44	20.9	32	25		0.5	127.6
45	8.3	3	10		0.5	30.3
Total	29.2	35	35	0.0624		
44	24.7	27	62		0	43.4
47	27.8	105	70		1	150.4
Total	52.5	132	132	<0.0001		
45	26.9	0	130		0	0
47	76.3	501	371		1	135.2
Total	103.2	501	501	<0.0001		

Appendix 2. Data for rank calculation.

Table 2. Rank cross table for Rank 1, with index gained from appendix 2 table 1.

		W	I	N	N	E	R	S	
	ID	5	8	11	33	44	45	47	∑ Losses
L	5		0	0.5	1	0	0	0	1.5
O	8	1		1	0.5	1	0	0.5	4
S	11	0.5	0		0.5	0	0	0.5	1.5
E	33	0	0.5	0.5		0.5	0	1	2.5
R	44	1	0	1	0.5		0.5	1	4
S	45	1	1	1	1	0.5		1	5.5
	47	1	0.5	0.5	0	0	0		2
∑ Victories		4.5	2	4.5	3.5	2	0.5	4	

ID	5	8	11	33	44	45	47
Victories - Losses	3	-2	3	1	-2	-5	2
Rank order	5	2	5	3	2	1	4

Table 3. Ranking order for Rank 1. Victories minus losses is calculated from the sum of victories and sum of losses in the cross rank table for Rank 1. A high number in rank order equals a high rank.

Table 4. Rank order for Rank 2. Victories minus losses is calculated from the sum of victories and sum of losses in the cross rank table for Rank 2. A high number in rank order equals a high rank. This data is used to calculate Rank 3.

ID	5	8	11	33	44	45	47
Victories - Loses	284.4	-243.4	143.5	388.4	-247.9	-717.6	392.6
Rank order*	5	3	4	6	2	1	7

Table 5. Calculations of Rank 3. The difference between ID 5 and 33 is larger than between ID 33 and 47, therefore ID 5 gets the highest rank, and a unique rank. The difference between ID 33 and 47 is not larger than the difference between ID 47 and 11, therefore ID 33 and 47 will get the same rank, the second highest rank, and so forth.

ID	First rank-second rank...	First rank-second rank... (Rank index from rank 2)	Rank 2	Rank 3
47	47-33	4.2	7	3
33	33-5	104.0	6	3
5	5-11	140.9	5	3
11	11-8	386.9	4	3
8	8-44	4.5	3	2
44	44-45	469.7	2	2
45	-	-	1	1

Appendix 3. Group compositions

Table 1. Group composition for each of the observed GPS-marked female fallow deer in the study.

ID	Category	Average nr. of individuals	Standard Error	Min.	Max.
5	Total	60	3.749	3	300
5	Female	18	1.026	3	83
5	Male	6	0.409	0	37
5	Fawn	7	0.540	0	30
5	Unknown	32	3.396	0	265
6	Total	23	0.694	1	47
6	Female	18	0.504	1	37
6	Male	12	0.085	0	6
6	Fawn	2	0.107	0	8
6	Unknown	2	0.107	0	5
8	Total	64	1.568	5	100
8	Female	47	1.257	4	70
8	Male	2	0.368	0	19
8	Fawn	13	0.394	1	23
8	Unknown	8	0.488	0	41
11	Total	53	1.315	6	155
11	Female	34	0.981	5	100
11	Male	0	0.030	0	2
11	Fawn	14	0.403	1	45
11	Unknown	5	0.168	0	14
33	Total	130	4.339	2	293
33	Female	86	2.878	15	177
33	Male	13	0.853	0	42
33	Fawn	19	0.628	3	53
33	Unknown	14	0.458	0	31
44	Total	69	5.873	2	303
44	Female	46	3.536	1	177
44	Male	8	0.933	0	52
44	Fawn	11	1.059	0	53
44	Unknown	5	0.450	0	21
46	Total	21	0.528	8	36
46	Female	12	0.471	3	24
46	Male	7	0.325	0	17
46	Fawn	2	0.125	0	6
46	Unknown	0	0.047	0	2
47	Total	106	1.423	16	211
47	Female	43	1.038	8	87
47	Male	10	0.306	0	29
47	Fawn	18	0.424	2	47
47	Unknown	35	1.323	0	141

* Because of the different sample in the calculation of group composition and group size, the average group size does not equal the exact sum of females, males, fawns and unknown in all female groups.

Appendix 4. Mean distance to preferred habitat.

Table 2. Mean distance to each preferred habitat for each GPS-marked female fallow deer.

ID	Habitat	Mean dist. (m)	Std. Err.	Min.	Max.	Rank
5	Arable	476	80.202	39	640	7
8	Arable	493	159.854	131	1087	3
11	Arable	676	199.200	477	876	4
33	Arable	510	127.611	205	759	6
44	Arable	207	66.663	5	461	2
45	Arable	1096	208.051	312	2004	1
47	Arable	295	31.178	236	342	5
5	Broad-leaved	474	31.783	57	803	7
8	Broad-leaved	503	34.534	71	1097	3
11	Broad-leaved	997	41.399	368	1631	4
33	Broad-leaved	701	48.251	84	1083	6
44	Broad-leaved	621	44.891	24	1387	2
45	Broad-leaved	1044	52.314	57	2105	1
47	Broad-leaved	578	32.160	186	1179	5
5	Younger	461	28.172	18	784	7
8	Younger	536	27.644	57	1175	3
11	Younger	959	28.791	334	1629	4
33	Younger	691	32.994	66	1087	6
44	Younger	601	34.204	64	1423	2
45	Younger	982	36.697	32	2219	1
47	Younger	577	26.760	212	1152	5